THE CHROMOSOMES OF ACHOLLA MULTISPINOSA.[1]

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In a recent paper entitled "Some New Types of Chromosome Distribution and their Relation to Sex," I described in part the history of the chromosomes in *Acholla multispinosa*. At that time, I had but little material and was unable to say with certainty just what occurred in the second maturation division. However, I stated that all the evidence pointed to the conclusion that the ten chromosomes in the ring divided equally while the members of the hexad group in the middle remained undivided, five of them passing to one pole, and one to the other. I also stated that the number of chromosomes and their size relations in the male and female somatic cells made it almost conclusive how the members of the hexad group separated; that no other manner of distribution could give an end result of 26 chromosomes for the male and 30 for the female.

In order to clear up the doubtful points, I collected new material in larger quantities during the past summer and fortunately have been able to follow the complete history of the chromosomes in the spermatogonial, oögonial and the first and second maturation divisions. As a result, I can state that my former observations were entirely correct and that my inference in regard to the separation of the chromosomes in the second division has proven true.

The oögonial divisions (Fig. 1, *A*, *B*, *C* and *D*) show 30 chromosomes, 24 of which are approximately the same size while six are much smaller. I have examined female material from New Jersey, New York, Indiana and Illinois and they all show the same number and size relations. The spermatogonial groups (Fig. 1, *E*, *F*, *G* and *H*), on the other hand, contain 26 chromosomes, 22 medium sized, one very large and three small. Since the number and size relations of the chromosomes in the male and female groups are so different, it might be argued that I have been working with two species. In regard to this question, I

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wish to state that with this point in mind, Van Duzee has examined my material very carefully and that the larger part of it (30 specimens) consisting of both males and females was collected within a small circular area of about 200 feet in diameter.

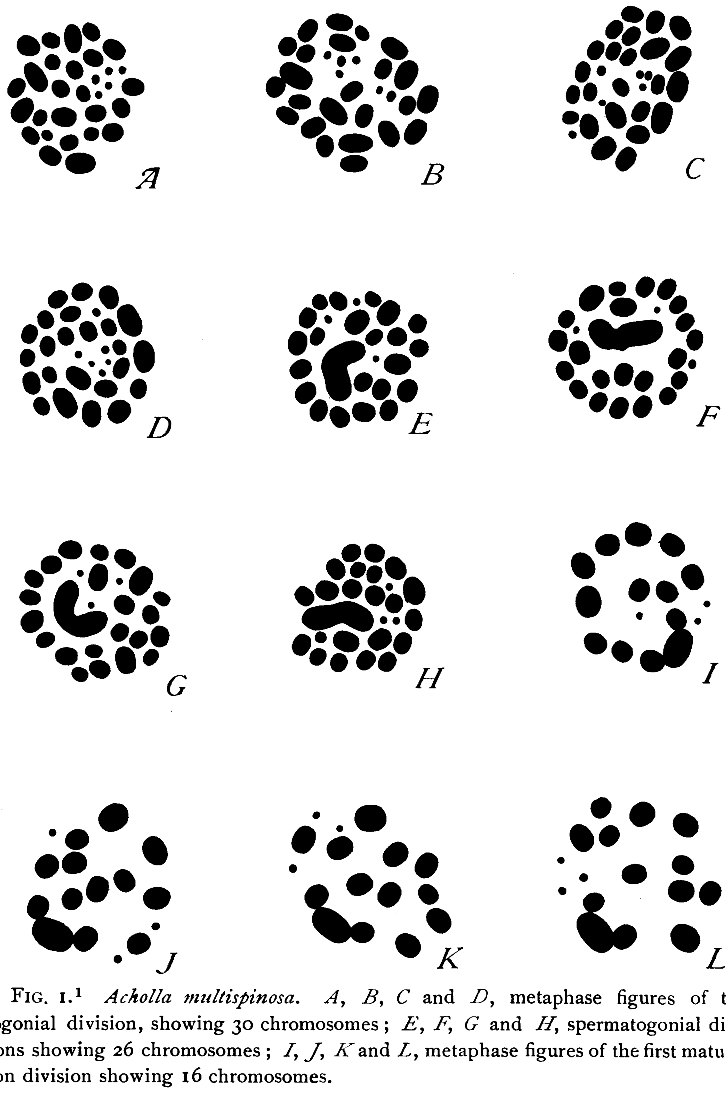

FIG. 1.[1] *Acholla multispinosa.* *A*, *B*, *C* and *D*, metaphase figures of the oögonial division, showing 30 chromosomes; *E*, *F*, *G* and *H*, spermatogonial divisions showing 26 chromosomes; *I*, *J*, *K* and *L*, metaphase figures of the first maturation division showing 16 chromosomes.

The metaphase plate of the first spermatocyte-division shows 16 chromosomes (Fig. 1, *I*, *J*, *K* and *L*). As 26 is the spermato-

[1] All figures are drawn to the same scale and magnified 1,500 diameters.

gonial number, ten of these must be bivalent and six univalent. The three small ones are again present. The large one is here as in the prophase of the first division linked end to end with two other chromosomes. All divide equally in this division. I was fortunate enough to find a side view of the anaphase showing all three small ones dividing (Fig. 2, *D*). The large one and the two

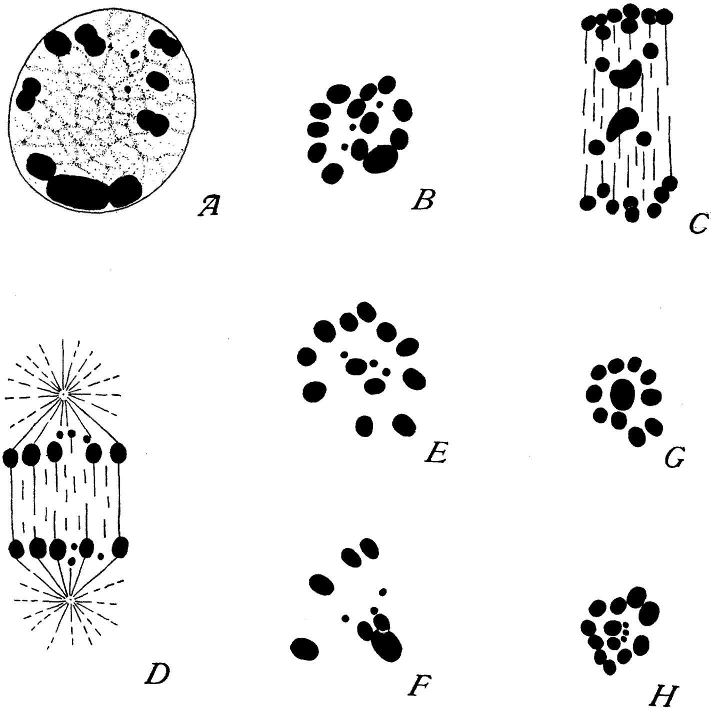

FIG. 2. *Acholla multispinosa*. *A*, prophase of the first division; the large chromosome is joined end to end with two others; *B*, anaphase, polar view, of the first division; *C*, anaphase, side view, of the first division, showing the late division of the large chromosome and the two with which it is linked; *D*, anaphase, side view of the first division, showing the division of the three small chromosomes; *E*, metaphase of the second division, polar view, showing the ten chromosomes in the ring and the five members of the hexad group which lie in one plane; *F*, a slightly oblique view of the second division metaphase showing the hexad group; *G* and *H*, anaphases, polar view, of the second division, showing the chromatin content of the two classes of spermatozoa.

with which it is joined are usually the last to divide (Fig. 2, *C*, a side view of the first division anaphase). Fig. 2, *B*, is a polar view showing 16 chromosomes. There is no definite arrange-

ment in this division, although the large one always lies on the periphery.

As a result of the equal division of all the chromosomes in the first division, the metaphase plate of the second maturation division shows 16 chromosomes. In this division, however, there is always a definite arrangement. Ten of the 16 form a more or less regular ring while the remaining six, two medium sized, three small and the extra large one, are arranged in a hexad group in the middle. Five members of the hexad group, the two medium sized and the three smaller ones, lie in one plane, while the sixth member, the large chromosome, lies either above or below the five on the other side of the equatorial plane. Fig. 2, *F*, is a view of the second division metaphase, slightly to one side, showing the arrangement of the hexad group. Fig. 2, *E*, shows the ten chromosomes in the ring and the five in the middle. The large one could not be shown without displacing it. The ten chromosomes in the ring divide equally while the members of the hexad group do not divide, but five of them, the two medium sized and the three small ones, pass to one pole and the large one to the opposite pole. The anaphases showing this unequal distribution are shown in Fig. 2, *G* and *H*. Two classes of spermatozoa are thus produced, differing in that one class contains 15 chromosomes, the other 11. Further, since the oögonial number is 30 and the spermatogonial 26, the reduced number of chromosomes in the egg must be 15 and the two classes of spermatozoa must be respectively male and female producing.

Spermatozoön 15 + egg 15 = 30 (♀)
Spermatozoön 11 + egg 15 = 26 (♂)

As stated in the previous account, the size relations of the chromosomes serve as an aid in reaching the above conclusions. If the fifteen-chromosome class of spermatozoa meets an egg with 15 chromosomes, three of which are small, the offspring should have 30 chromosomes, six of which should be small. This is what we find in the female cells. If the eleven-chromsome class of spermatozoa meets the same egg, the cells of the embryo should have 26 chromosomes, three of which should be small and one extra large. This condition is fulfilled in the male cells.

I have not been able to follow the history of the differential chromosomes during the growth period. A plasmosome is present. Sometimes it stains perfectly black but again it may stain much as the cytoplasm does. If the latter, a number of chromatin bodies can be seen embedded in it. As I have followed the history of the plasmosome and its relation to the differential chromosomes in *Prionidus* it seems very probable that here, too, in *Acholla* the differential chromosomes are embedded in the plasmosome during the growth period.

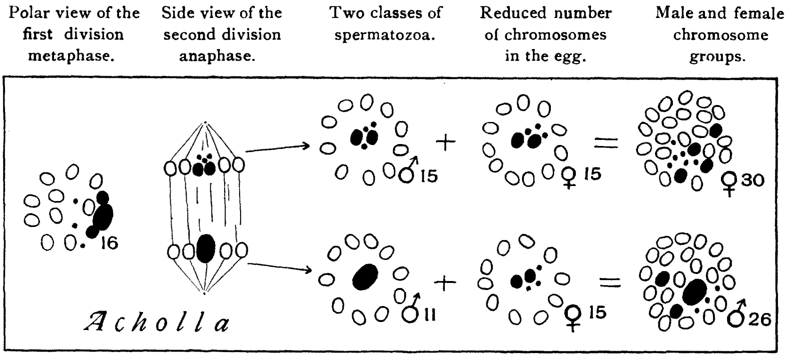

FIG. 3.

Fig. 3 gives a diagrammatic representation of what occurs in maturation and fertilization.

Only a few years ago maturation meant a reduction to one half; the number of oögonial and spermatogonial chromosomes were thought to be the same in each species and this number an even one. Even as late as 1900, Wilson in "The Cell in Development and Inheritance" writes as follows: "Van Beneden's epoch-making discovery that the nuclei of the conjugating germ-cells contain each one half the number of chromosomes characteristic of the body-cells has now been extended to so many plants and animals that it may probably be regarded as a universal law of development." Those who believe that the odd chromosome is merely a delusion in the minds of a few investigators still cling to the universality of Van Beneden's law. However, the law is no longer of universal application. Not only the odd chromosome but a number of other irregularities have been recently described,

the present case of *Acholla* giving the greatest variation in number. In fact so many variations have been found that we may justly ask what is to be the limit of these irregularities and where will they lead us?

The case of *Acholla* is interesting for two principal reasons. First, it gives us the greatest variation in number so far discovered, there being a difference of four between the male and female groups. Secondly, if we examine the size relations carefully it will be noticed that the large chromosome which goes to the male-producing pole seems to contain a larger amount of chromatin than the five chromosomes of the hexad group which go to the female-producing pole. A number of measurements show this to be the case. In all the irregularities hitherto described, the female cells contain the larger number of chromosomes and also the greater quantity of chromatin. The present case is not an exception to the number but seems to be in regard to the quantitative relations.

Several recent theories of sex determination have been based upon the quantitative relation of the chromatin. The evidence in *Acholla* forms one of the stumbling blocks in the way of some of these interpretations. To be sure, if we should ignore the large chromosome, the homologue of the small idiochromosome, or what Wilson terms the *Y* element, many difficulties would disappear. Most certainly though, as Morgan says, there is no reason for disregarding it except that its presence, in an active condition, does not fit in with our hypothesis. In his recent paper on "Sex Determination in Phylloxerans and Aphids," Morgan while realizing the difficulties in its way, further develops the quantitative hypothesis and holds to it as a rough approximation to a solution. In regard to the case of *Acholla* he suggests that possibly the five chromosomes of the hexad group which go to the female-producing pole are more active than the large chromosome which goes to the male-producing pole. The suggestion may be true, but is the question of the activity of the chromosomes the same as that of the quantitative relations?